

ECHOLOCATION OF FLYING INSECTS BY THE BAT, *CHILONYCTERIS PSILOTIS*

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Among the many aspects of acoustic orientation in bats that have been analyzed, studies of sonar design as it varies during insect pursuits and obstacle avoidance have been limited to a few genera, principally of vespertilionid bats (Griffin, 1953, 1958; Grinnell and Griffin, 1958; Griffin, Webster, and Michael, 1960; Cahlander, McCue, and Webster, 1964; Webster, 1963; Griffin, Friend, and Webster, 1964). Griffin (1962) has also reported briefly on pursuit behavior in *Noctilio* (Noctilionidae) and *Rhinolophus* (Rhinolophidae). Recently we have observed echolocation during insect pursuits in *Pteronotus* (Novick, 1936b) and in *Chilonycteris parnellii* (Novick and Vaisnys, 1964), closely related bats of the subfamily Chilonycterinae (Phyllostomatidae).

Systematic alterations in pulse duration and interpulse interval (or pulse repetition rate) have been described in *Pteronotus* and *C. parnellii* which imply a dependence, for detection of insect prey, on pulse-echo overlap at the bat's ear and which further imply the value to these two bats of adjusting pulse duration relative to target distance so as to give fairly constant pulse-echo overlap sequences during insect pursuits. Such apparent utility of pulse-echo overlap encourages consideration of the possibility of the bat's using a variety of analytical methods which have been briefly discussed by Pye (1960, 1961a, 1961b), Kay (1961, 1962), and Novick and Vaisnys (1964). The systematic variations in pulse duration have also implied measurement of target distance since pulse duration has, during a part of each pursuit, varied directly proportionally with bat-target separation. Variations in interpulse interval may be related to reaction time in the central nervous system and/or conservation of output.

The sonar design of *C. parnellii* differs strikingly from that of *Pteronotus*, as, indeed, it does from *C. psilotis* (Griffin and Novick, 1955; Novick, 1963a). These differences in design, principally pulse duration and intensity, increased our interest in comparing the behavior of the members of this closely related group of bats, in the hope of unveiling some of the functions of the sound parameters used.

The orientation sounds of one individual *Chilonycteris psilotis* Dobson (Phyllostomatidae) (Hall and Kelson, 1959) were recorded while the bat flew around a laboratory flight room and pursued and apparently captured common fruit flies, *Drosophila* sp. The orientation of *C. personata* has previously been studied by Griffin and Novick (1955) and Novick (1963a). This bat is either the same as *C. psilotis* or a very close relative. These bats are delicate in captivity. Of several individuals captured in a cave at Lake Tequesquitengo, Morelos, Mexico, only one survived to pursue fruit flies in New Haven and this one did so for less

than a week. I am grateful to Dr. O'D. W. Henson, Jr. and Mr. R. M. Holt for capturing and maintaining this bat, to Dr. B. Villa-R. for his advice and aid, to the Institute of Biology of the National University of Mexico for the use of their facilities and to the Mexican government for permission to capture and transport this bat. This work was supported in part by the National Institute of Mental Health and by the Air Force Office of Scientific Research.

The bat's orientation sounds were recorded with a custom-made Granath microphone and a Precision Instrument Pi-202 tape recorder. Nine hunting sequences were chosen for analysis because of their high signal-to-noise ratio and completeness. These were analyzed chiefly from filmed oscillograph tracings. A Kay Electric Co. sound spectrograph was also used.

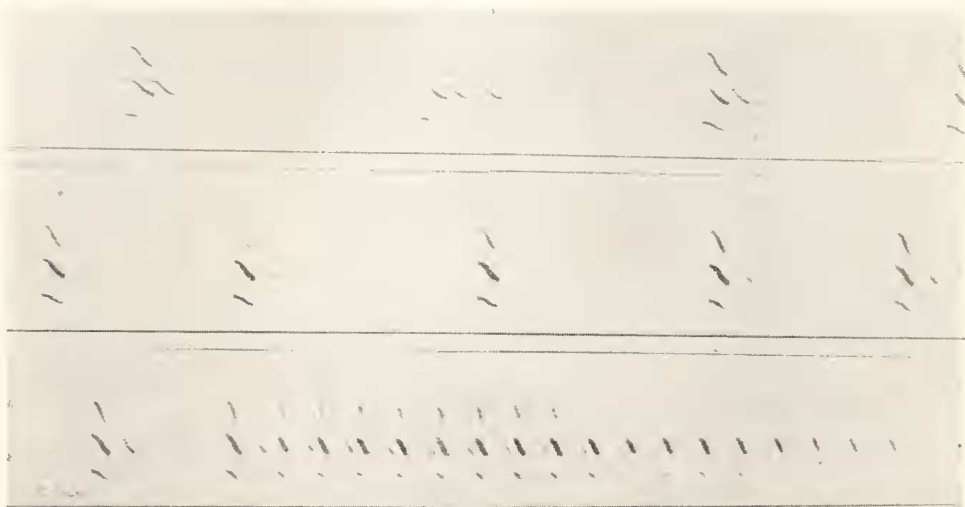


FIGURE 1. A sound spectrogram of the orientation pulses of *C. psittotis* during a fruit fly pursuit. The three strips are sequential with the last pulse of each repeated at the beginning of the next strip to increase clarity. Frequency is shown vertically; time horizontally. Echoes of many of the pulses appear as fainter duplicates a few milliseconds later. Note the three frequency components, the change in frequency drop during the pursuit, and the systematic changes in pulse duration and interpulse interval.

The present analysis deals chiefly with the significance of variations in pulse duration, interpulse interval and/or pulse repetition rate, and frequency pattern as seen in these records of insect pursuits, and with calculated pulse-echo overlaps. As in the vespertilionids (Griffin, Webster, and Michael, 1960), *Pteronotus* (Novick, 1963b), and *C. parnellii* (Novick and Vainsys, 1964), these pursuits may be subdivided into search, approach, and terminal phases (Figure 1).

The search phase cannot yet be distinguished, in the case of any bat, from other normal, cruising orientation sound sequences. Presumably, during this phase, the bat has no knowledge of the insect it is yet to pursue or, at least, takes no observed behavioral notice of such. Clearly, a cruising bat is receiving information from a complicated laboratory environment (either as echoes or lack of echoes or as echoes of uninteresting timing) and the bat must be adjusting its flight so

as to avoid walls and ceiling, etc., but we have not yet recognized patterns of behavior in cruising flight other than an apparent varying regularity. Two such long, cruising sequences, recorded at high amplitude and lacking patterns suggesting insect pursuit, have been analyzed. These lasted 770 and 870 msec., respectively. Pulse durations of 2.9 to 4.8 msec. occurred, with a mean of 4.0 msec. Interpulse intervals (the silent period between pulses) varied from 44 to 84 msec. with a mean of 56 msec.; almost all lay between 44 and 65 msec. The repetition rate was about 17–18 pulses per second in both series. Thus, searching flight in *C. psilotis* seems to consist of a sequence of pulses about 4 msec. in duration, spaced about 60 msec. apart.

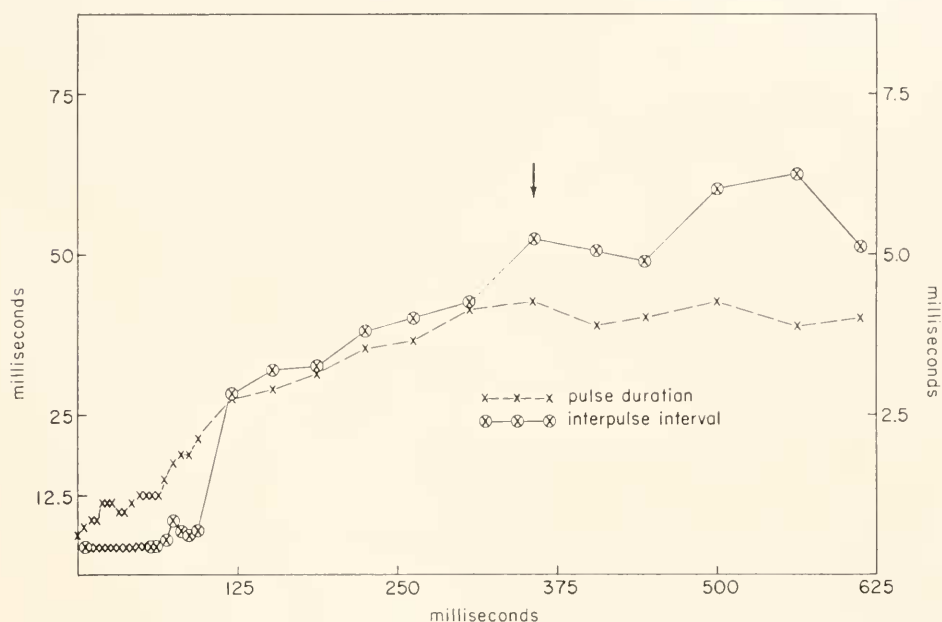


FIGURE 2. An example of a fruit fly pursuit by *C. psilotis*. Pulse duration and interpulse interval are plotted against milliseconds before the end of the pursuit. One msec. = 1.73 mm. (see text). The arrow indicates the first calculated pulse-echo overlap. Note that in Figures 2 through 5, time reads from right to left (larger numbers represent earlier events).

The approach phase begins, by definition, in these analyses, at the point at which we first recognize that the bat is committed to a complete pursuit. In *Pteronotus* (Novick, 1963b), this point was recognized by the first obvious shortening of the interpulse interval. Systematic changes in pulse duration also occurred, but their initiation point was harder to pinpoint. In *C. parnellii* (Novick and Vaisnys, 1964), the beginning of the approach phase is signaled by an increase in pulse duration while changes in interpulse interval occur gradually and are initially hard to identify. In *C. psilotis*, the beginning of the approach phase is marked by shortening of both pulse duration and interpulse interval (Figs. 1 and 2). During the approach phase, the bat apparently clarifies the position, nature, and velocity of the target and sets its own flight path for interception.

When plotted against time, close to linear shortening of the pulse duration and interpulse interval characterize this phase. It terminates sharply in a transition to a series of evenly spaced, short pulses of high repetition rate called the terminal phase (Figs. 1 and 2). In the terminal phase, the bat presumably closes in on, captures, and begins to eat the insect. Following the terminal phase there is a long silent period and then a return to searching sound production.

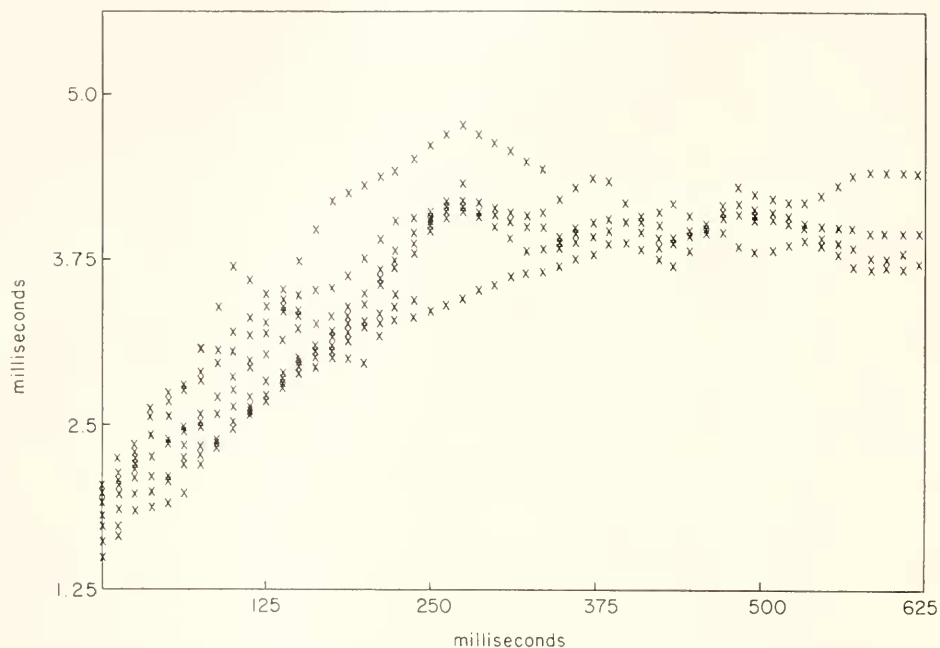


FIGURE 3. Nine fruit fly pursuits by *C. psilotis*. The pursuits have been synchronized by assuming equality of situation at the beginning of the terminal phase which is shown here as zero. Pulse durations preceding the beginning of the terminal phase are plotted against time during the pursuit. Intermediate interpolated values (between pulses) are plotted for equal time intervals. Note the change in the distribution of points at about 250 msec. before the beginning of the terminal phase. One msec. = 1.73 mm.

The nine best pursuits recognizably occupy 190 to more than 350 msec., measured from the pulse preceding the first recognized decrease in pulse duration. If the pulse preceding the first recognized decrease in interpulse interval is used instead as the index, the same pursuits last 210 to 360 msec. Durations, by both criteria, of about 300 msec. are the most common. The terminal phase, identified by short interpulse intervals, occupies 28 to 94 msec. of this time. Excluding one terminal phase which is so short that it seems possible that the target escaped, the range is 50 to 94 msec. Thus, the approach phase *per se* ranges from about 150 to 290 msec. The measurements are objective except for the need to choose inflection points—the beginnings of the approach and terminal phases.

If one plots all of the pursuits (pulse duration and interpulse interval vs. time) together by assuming that the beginning of the terminal phase in each

case represented somewhat the same situation to the bat (perhaps a given range from the fly or perhaps a clear bearing) and that the bat's flight speed was uniform and constant, then mean pulse duration or interpulse interval at any point in time from the fly can be calculated. The first discernible decrease in mean pulse duration occurs at about 225 msec. before the beginning of the terminal phase (about 300 msec. before the end of the pursuit) (Fig. 3). Using mean interpulse interval, the first discernible drop may be at about 240 msec. and is

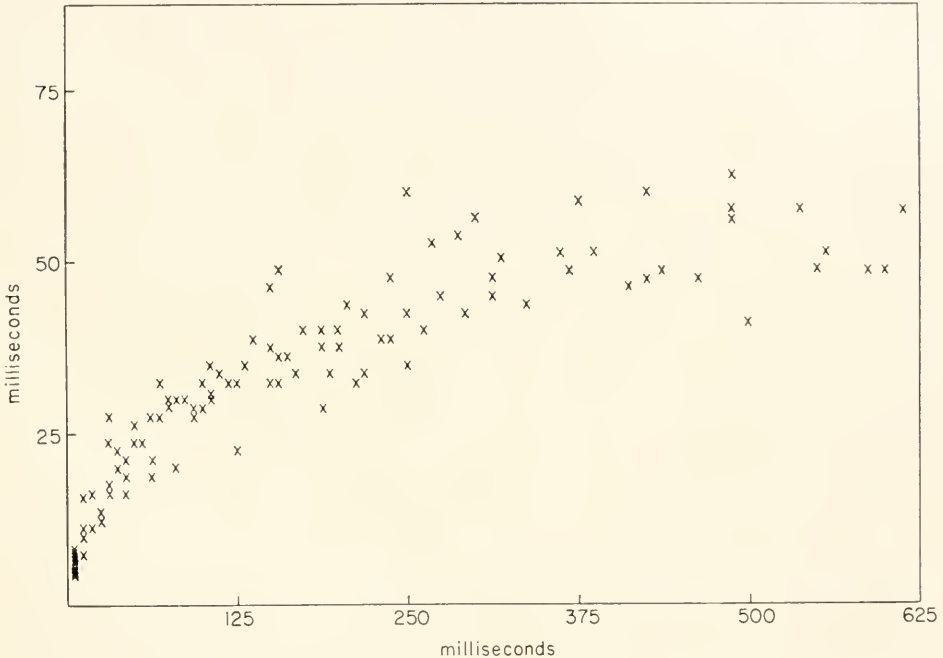


FIGURE 4. Nine fruit fly pursuits by *C. psilotis* have been synchronized and plotted together by assuming equality of situation at the beginning of the terminal phase. The duration of interpulse intervals (represented as events occurring at the beginning of the pulse preceding the interval) are plotted against time during the pursuit, setting the beginning of the terminal phase as zero. Note the transition immediately to the left of 250 msec. One msec. = 1.73 mm.

certain by 225 msec. before the beginning of the terminal phase (Fig. 4). By these various criteria, therefore, a common value for the approach phase would be about 240 msec., for the terminal phase about 55 msec. Note that the entire terminal phase transpires in an interval comparable to a single interpulse interval of the search phase!

A complete analysis, knowing only the time separating the moving bat from its moving target, is impossible. Unfortunately, we did not have facilities for photographing these pursuits nor do we have an objective measure of the bat's flight speed. Time, however, can be converted to distance if several assumptions and approximations are allowed. First, an empirically chosen flight speed of 1.73 m./sec. has been assigned to this bat. Second, we assume the bat's velocity

relative to the fly to be constant throughout the pursuit. And, finally, we assume that the pursuit ends with a capture or that the last pulse represents a zero point from which the distance separating the bat and fly can be calculated back for each previous pulse. We know the bat's velocity is not constant. During pursuits, bats appear to change direction as well as speed. We have no useful information about the flies but their directions of flight are probably random relative to the

TABLE I

Various parameters of insect pursuits by three closely related species of bats. The data for Pteronotus are from Novick (1963b); those for C. parnellii are from Novick and Vaisnys (1964).

	<i>C. psilotis</i>	<i>Pteronotus</i>	<i>C. parnellii</i>
Search phase			
pulse duration (msec.)	2.9-4.8	3.9-5.0	14-26
interpulse interval (msec.)	44-84	70-200	20-60
repetition rate (pulses/sec.)	17-18	10-12	ca. 14
Duration of pursuit			
time (msec.)	210-360	550-620	560-740
distance, calculated (mm.)	360-620	690-790	ca. 3,300
Approach phase			
duration in time (msec.)	150-290	350 (mean)	380-560
duration in distance, calc. (mm.)	260-500	440 (mean)	2,400 (mean)
number of pulses	5-9	3-10	7-10
pulse duration (msec.)	decreasing to 1.5-2.1	decreasing to 2.4-3.2	rising from 20-21 to 28-37 and then falling to 23-27
interpulse interval (msec.)	decreasing from 40-7	decreasing from about 50 to about 25	fluctuating about 20-50 and then decreasing to 4-5
final repetition rate (pulse/sec.)	about 100	about 35	about 20 or slightly more
pulse-echo overlap (msec.)	ca. 1.2	ca. 1.5	ca. 20
Terminal phase			
duration in time (msec.)	50-94	150-214	180-190
duration in distance, calc. (mm.)	90-160	190-270	800-900
number of pulses	11-18	27-39	9-12
pulse duration (msec.)	decreasing to 0.6-1.0	decreasing to 1.0-1.25	decreasing to 6-8
interpulse interval (msec.)	4.5-5	4.5	2.5
final repetition rate (pulses/sec.)	ca. 170	ca. 200 or more	ca. 80-100
pulse-echo overlap (msec.)	0.8-0.9	ca. 1.0	decreasing from 18 to ca. 5
Theoretical range (based on calculated pulse-echo overlap and flight speed)	400-700 mm.	680-860 mm.	3,800 mm.
Flight speed (mm./msec.)	1.73	1.25	4.5

bat (unless they take evasive action as do some moths; Roeder and Treat, 1961) and their speed is probably small compared with that of the bat. In any event, we have ignored the movement of the flies in these analyses. The flight speed of 1.73 mm./msec. was initially arrived at by plotting pulse duration *vs.* time from the end of the pursuit and arbitrarily seeking a flight speed which would yield a regular pattern of calculated pulse-echo overlap when time was converted to distance. The flight speed is consistent with known bat flight speeds and is independently confirmed by correlation (cited below) between first calculated pulse-echo overlap and first behavioral response as well as by its yielding regular patterns of pulse-echo overlap in all 9 pursuits. We have discussed, elsewhere, these extrapolations which have previously proved useful (Novick, 1963b; Novick and Vaisnys, 1964).

Fixing the bat's position at zero, then, at the end of the terminal phase, we have calculated its position at the beginning of each pulse during each pursuit. We find that the approach phases begin at about 500 mm. (360 to 620 mm.) from the fly and that the terminal phases begin from 90 to 160 mm. from the fly. The approach phase alone therefore occupies about 400 mm. (260 to 500 mm.) (Table I).

Having calculated the bat's position relative to the fruit fly, one can calculate the time taken for sound to cover the roundtrip distance (using 350 mm./msec. as the speed of sound). Knowing the pulse durations being used, one finds that the first pulse-echo overlap would occur at 230 to about 440 msec. or about 400 to 700 mm. before capture. The first pulse-echo overlap would normally be of very short duration (about 0.3 msec.). If the bat is flying at 1.73 mm./msec. and if the searching repetition rate is such that each pulse and its subsequent silent interval occupy about 60 msec., then the bat will have moved about 100 mm. between pulses. Neglecting the fly's movement, the round trip distance is decreased by 200 mm. Sound covers this distance in 0.6 msec. Thus, if the echo from a given fly just fails to overlap with one pulse, it will, on the average, overlap by 0.6 msec. with the next. Provided the bat did not respond to non-overlapping echoes by lengthening pulse duration (no apparent evidence in *C. psilotis*) the average first overlap would therefore be about 0.3 msec. The average second overlap would be about 0.9 msec., provided the bat had not already altered its behavior in response to the first overlap. If about 0.5 to 1 msec. of overlap is needed for the bat to perceive or take an interest in an echo, the first pulses providing such information occur at 340 to 670 mm. Thus, the first substantial pulse-echo overlap occurs at about the same time that the last normal interpulse interval is being produced (360 to 620 mm.). The coincidence of these values—the interpulse interval which is completely objective and the calculated first significant pulse-echo overlap—tends to justify the assumptions made above which allowed these extrapolations. Similar relationships have been reported in *Pteronotus* and *C. parnellii* (Novick, 1963b; Novick and Vaisnys, 1964).

Specifically, the first calculated pulse-echo overlap precedes the first behavioral response by 34 to 150 msec. This puts vague limits on apparent response time. The range of values may well reflect the extrapolation error. In *C. parnellii*, where flight speed was objectively recorded, a possible response time of 130 to 150 msec. was reported (Novick and Vaisnys, 1964). Grinnell's (1963a, 1963b)

studies of brain responses to acoustic stimuli in anesthetized vespertilionid bats suggest that cortical decisions may be involved in these initial echo recognitions. In subsequent portions of pursuits, time seems to be lacking for higher level judgment.

The first, second, or third pulse following the first calculated pulse-echo overlap is distinguishably shorter than the searching pulses. Thereafter, pulse duration decreases close to linearly when plotted *vs.* time or distance separating the bat and fly. The slope of this line varies in different pursuits from 1 msec. of shortening of pulse duration per 100 mm. of apparent reduced separation to 1 msec./350 mm. These different slopes may indicate different closing speeds of bat on insect (as, for example, if the insect is flying directly toward rather than directly away from the bat). In all pursuits, however, the relationship is linear during the approach phase. Pulse duration drops from average values of about 4.0 to 4.2 msec., initially, to values of 1.5 to 2.1 msec. at the beginning of the terminal phase.

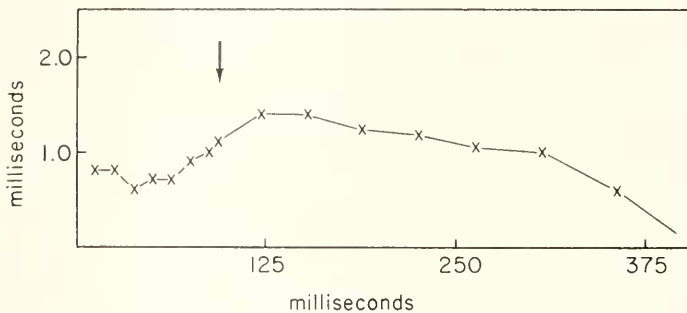


FIGURE 5. Pulse-echo overlap in the longest, recorded single fruit fly pursuit by *C. psilotis*. Note the rapid rise of pulse-echo overlap to values of 1.0 to 1.4 msec. during the approach phase and the shift to values of 0.6 to 0.8 during the terminal phase. The arrow indicates the beginning of the terminal phase. The calculated pulse-echo overlap is shown for each pulse during the approach phase but a representative value is shown for each 12.5 msec. during the terminal phase to increase clarity.

As has been the case in *C. parnellii*, pairing of pulses in the late approach phase sometimes occurs. That is, two pulses of close to the same duration are followed by two of shorter but almost equal duration and so on. Such pairs may be the functional units. The governing feature, here, may be reaction or decision time (that is, that decisions concerning revision of pulse duration take longer to make than the time available between single pulses—about 25 msec. or less), or pairs may actually be functionally desirable (as, for example, to assess direction by exploiting the movement of the head between the two pulses which, because of beaming and directionally tuned ears, would alter the echo intensity).

The speed of sound is constant, the bat's flight speed has been assumed constant, and pulse duration *vs.* time or distance drops linearly. When one calculates the successive pulse-echo overlaps, therefore, these prove to remain constant throughout the approach phase after an initial rapid rise. Thus, at 390 mm. from the fly, where all nine pursuits have calculated overlap values, the range of over-

lap is 0.4 to 1.7 msec. with a mean of 1.0 msec. At 300 mm., the range is 0.6 to 1.5, mean 1.1 msec.; at 170 mm., range 0.9 to 1.6 msec., mean 1.2 msec. In individual pursuits, the value is remarkably constant. Variations of less than 0.5 to 0.6 msec. are the rule during the approach phase. The characteristic individual approach phase overlap levels of the respective pursuits are 1.1, 0.9, 1.2, 1.6, 1.2, 0.9, 1.1, 1.2, and 1.2 msec. (Fig. 5).

During the approach phase, then, pulse duration drops off linearly from about 4.0 to 4.2 msec. to about 1.4 to 2.1 msec. as the pulse-echo overlap levels out at about 1.2 msec. During this time, interpulse interval also drops sharply but not linearly. Search phase interpulse intervals of about 56 msec. yield to intervals averaging about 40 msec. between 200 and 270 msec. before the beginning of the terminal phase; to 31 msec. between 95 and 125 msec.; to 21 msec. between 30 and 60 msec.; and to about 12 msec. between 13 and 30 msec., respectively, before the beginning of the terminal phase. The last interpulse interval of the approach phase or, perhaps, the first of the terminal phase is about 7 msec. in duration with little variation from one pursuit to another (Fig. 4).

The repetition rate, about 17–18 pulses/sec. during the search phase, has increased to about 110/sec. by the end of the approach phase. The approach phase in *C. psilotis* varies in these analyzed pursuits from 5 to 9 pulses in length.

The terminal phase in *C. psilotis* is grossly distinguishable from the approach phase. The interpulse interval drops immediately to a minimal value of about 4.5 to 5 msec. and remains at that level throughout. The pulse duration also drops from initial values of about 1.3 to 1.9 msec. to terminal values of 0.6 to 1 msec., without a dramatic shift from the previous linear drop of the approach phase until values of 1.0 to 1.3 msec. are achieved, after which the pulse duration curve flattens out and appears to approach a limit. Excepting one example, there were from 11 to 18 pulses in the terminal phase. In the exceptional case only 7 pulses appeared. This might have represented a rapid catch or a miss. The terminal pulse repetition rate, on the average, is about 170 pulses/sec.

The transition from approach phase to terminal phase is generally non-ambiguous and is most clearly defined by a break in the interpulse interval τ s. time curve. The interval just before the transition one is from 2 to 4 times as long as the interval just after the transition one. During the terminal phase, calculated pulse-echo overlaps are shorter than during the approach phase but again are uniform and regular with values ranging from about 0.6 to 1.3 msec. At a distance of 90 mm., the overlap averages 0.9 msec.; at 65 mm., it averages 0.8 msec.; at 45 mm., 0.8 msec.; and at 20 mm., 0.9 msec. (Fig. 5).

Sound spectrographs of pulses selected from search, approach, and terminal phases universally show a fundamental initially of about 21 kcps accompanied by its second, third, and fourth harmonics of 42, 63, and 84 kcps, respectively. The fundamental frequently appears faint. Either the second or, more often, the third harmonic is at the highest amplitude, especially during the terminal phase (Fig. 1).

The initial frequency varies slightly from pulse to pulse (perhaps by 1 kcps), but does not vary systematically during a pursuit. The last pulses are essentially like the first in frequency components.

During the course of a pursuit, however, the frequency pattern changes. In every case, the frequency drops during a pulse. The fundamental in search phase

pulses drops to 17 kcps at the end of the pulse while the harmonics drop to multiples of 17. The same 21 to 17 kcps fundamental frequency drop seems to characterize all of the pursuit pulses. The slope of the drop, however, changes. In the search phase, the initial 1.3 to 1.5 msec. of each pulse seem to be close to constant in frequency. The final 1.0 to 1.3 msec. or so seem also to be constant in frequency or, at least, of very shallow slope. The frequency drop occurs during the central part of the pulse (Fig. 1).

The first apparent change in the frequency pattern is a change in slope of the final portion of the pulse which shifts, from being constant in frequency, to fusing more and more with the central pulse portion, but can still be distinguished by an inflection point in the early terminal phase, after which it can no longer be clearly identified.

The initial constant frequency portion shortens during the approach phase and also starts to have a frequency drop, though at a different slope from the rest of the pulse. The drop becomes more marked and fuses with the rest of the pulse early in the terminal phase. The central, frequency modulated portion remains much the same throughout a pursuit.

Thus, during the search phase, the frequency pattern has a lazy Z shape (Fig. 1). During the approach phase, the curve becomes sigmoid, and during the terminal phase looks like a slash mark. The frequency vs. time curve even in the terminal phase may not be a straight line, but the resolution of our equipment does not reveal any clear and regular inflection points.

DISCUSSION

The constant or almost constant frequency portions of the search and early approach phase pulses may provide markers for distance identification. In any event, if our calculations are approximately correct, the usual pulse-echo overlap, here about 1.2 msec., would tend to consist of an echo of constant fundamental frequency of about 21 kcps overlapping with an outgoing constant frequency portion of 17 kcps. During the search phase, at least three kinds of echoes could easily be distinguished. Those just barely overlapping (about 1 msec.) would give a simple situation of two separate but constant frequency components. Closer objects would give pulse-echo overlaps involving the frequency modulated parts of the pulse and echo as well as the constant frequency parts. More distant objects would give no pulse-echo overlap. Thus, "too much" and "too little" overlap could be identified easily.

In the approach phase, the constant frequency portions are systematically changed. Soon they, too, show a dropping frequency and by the early part of the terminal phase are no longer identifiable. It should be possible for such differing frequency slopes to provide intra-pulse markers which could be used for distance measurement or for the assessment of closing speed relative to the pursued target. If these portions are, indeed, regular, then the bat may well use the pulse-echo overlap as a way of deciding whether it is at the expected distance from its target, or closing in on it faster or slower than anticipated, simply by noticing whether the overlap occurs during one portion of the pulse or another.

During the terminal phase, the typical pulse-echo overlap shifts to 0.8 msec. There is no clear marker at this time, though a poorly resolved change in fre-

quency may be present. If not, what does the constant pulse-echo overlap here signify and how is it measured and regulated? No answer is presently available.

Thus, the possibility presents itself that one purpose served by pulse-echo overlap is to measure distance and, perhaps, changing distance. Such a measurement would be independent of any knowledge of the speed of sound or the ability to discriminate short intervals of time. The initial detection in the search phase would simply give the information that there was a target at the standard specific detection range. Later information would confirm satisfactory closing speed.

If, indeed, the search pulses are designed with initial and final constant frequency portions in order to facilitate the recognition of echoes from a given useful hunting range, we still have to account for the frequency modulated character of the central portion. If the beginning of the pulse is to be different from the end, a frequency change must occur somewhere. The frequency change here may represent only that. Its slope may, instead, be the natural slope resulting from the relaxation of the laryngeal muscles in this bat. Other ways in which this frequency change may be exploited remain obscure.

The previous records of *C. parnellii* have been reexamined in a search for coincidence between pulse-echo overlap and frequency inflection points. In *C. parnellii*, almost the entire pulse is of constant frequency. Only the final 1 to 2 msec. show a frequency drop. Such a drop could well allow for initial detection during searching but would soon be only a small part of the typical 20-msec. overlap. In *C. parnellii*, note, however, that the typical pulse-echo overlap of 20 msec. equals the usual search phase pulse duration of 20 msec. and the 1-2 msec. frequency drop equals the frequency drop seen in *C. psilotis*. These may be coincidental but seem of possible interest. In any event, there is only an incomplete parallel with *C. psilotis*. Reexamination of the old records of *Pteronotus* does not permit more than a statement that the frequency pattern changes during pursuits. New examples will have to be recorded and analyzed.

In summary, all pulses seem to include about the same amount of frequency drop (perhaps, a result of the mode of sound production; Novick and Griffin, 1961). Search phase pulses are each, during an initial and a final 1.5-msec. portion, constant or almost constant in frequency. These constant frequency portions shorten during the pursuit and also incorporate, more and more, the standard frequency drop so that any clear separation between the initial and final pulse portions vs. the central pulse portion disappears by the early part of the terminal phase. These frequency patterns and their changes could provide target distance information during the pursuit by changing pulse-echo contrast. Such frequency changes would allow a three-quantity judgment of distance—just right, closer than expected, or further than expected. Such judgments could be translated into prediction of the target's relative flight path.

The data so far accumulated on the parameters of echolocation during insect pursuits by chironycterine bats are summarized in Table I. Some of the data from previous papers have been slightly recalculated or restated.

The closeness of these species of bats is exemplified by the decision of Burt and Stirton (1961) to include *Chilonycteris* in the genus *Pteronotus*. These authors felt that morphological considerations did not justify generic status, but other authors have disagreed and retain the two genera as we have chosen to do

here. All of these closely related bats were recorded pursuing a mixed group of *Drosophila* while flying in the same laboratory room. Thus, the targets and the auxiliary orientation problems, as well as the bat species, were similar. Flight speed, sound output design (frequency, frequency pattern, pulse duration, intensity, and interpulse interval) differed and presumably other parameters, not yet assessed, also varied. A comparison of the three performances, at this point, however, raises interesting but not yet answerable questions.

While searching, *C. psilotis* produces slightly shorter pulses than *Pteronotus*. Those of *C. parnellii* are 5 times as long. If pulse-echo overlap is needed for detection, pulse duration sets maximum range. Presumably flight speed also affects maximum practical range as must, indeed, pulse intensity. We can only observe for the moment that *C. parnellii* flies fastest and produces the loudest and longest pulses. Seemingly as a result, *C. parnellii* shows a fruit fly detection range of over 3 meters. *C. psilotis* produces the shortest pulses of these three species, giving it the smallest range of detection. This shortest pursuit distance, combined with faster flight than *Pteronotus*, results in the shortest pursuit duration (about $1\frac{1}{2}$ that of *Pteronotus* in time as well as in the number of pulses). Such a short pursuit involves many fewer decisions about the position of the fly and the bat's own flight control. Fewer decisions, of course, would seem to have been adequate since all of these bats seemed successful in their pursuits. If the range is small, the fly moves over a shorter distance during the pursuit. If the range is smaller, perhaps there is greater certainty about the position of the fly—its direction principally. The greater the range, the more problems would arise from confusing or ambiguous echoes. But probably, the greatest reason for the vastly greater number of pulses during *Pteronotus*' pursuits than during those of *C. psilotis* is that the bat flew more slowly and simply had to follow the fly for a longer time. One might reasonably ask why all these bats would not have hit on the same formula of pulse duration, intensity, and range. Flight speed itself might be the important difference but the size and flight habits of the common prey species might be even more important. All of these bats commonly occupy the same caves in large numbers. They seem to have very similar climatic demands. One might guess that they would hunt different insect populations and thus avoid competition. Insufficient information on their feeding habits precludes further speculation on this now. The striking anatomical difference in the wings of *Pteronotus* (which originate from the midline of the back as opposed to lateral attachment in almost all other bats) implies different flight habits.

The differences in interpulse interval (and, hence, repetition rate) may well reflect flight speed. In all three species, the repetition rate is such as to provide an apparently significant pulse-echo overlap from objects just beyond range of overlap with the previous pulse. Again flight speed seems to be a prime variable but there is also an apparent difference in the amount of overlap which draws the bat's attention. *C. psilotis* moves about 100 mm. between pulses, *Pteronotus* about 120 mm. and *C. parnellii* about 300 mm. Thus, objects just beyond overlap range from one pulse will yield about 0.6, 0.7, and 1.7 msec. of overlap, respectively, with the next pulse. The behavioral responses of each of these species suggest that this amount of overlap is enough to attract attention. The spacing of search phase pulses produced by each of these species is, however, surprisingly

similar, aside from the above considerations. Since the speed of sound is so great compared even with the swiftest of these three species, the common pulse spacing of about 50 to 75 msec. may simply reflect the length of the central nervous system path involved in searching decisions. Grinnell's (1963a, 1963b) recordings from vespertilionid bat brains may cast some light on these time relations.

The time consumed in an insect pursuit is remarkably similar in *Pteronotus* and *C. parnellii* but only $\frac{1}{2}$ as long in *C. psilotis*. In *C. psilotis* both the approach and terminal phases are shorter than in the other two bats. The approach phases in *Pteronotus* and *C. parnellii* are roughly equal in length as are the terminal phases. The savings in the approach phase for *C. psilotis* seem to come from the more immediate and consistent shortening of the interpulse intervals. The number of pulses is not noticeably different from that of the other bats. In the terminal phase, *C. psilotis* uses far fewer pulses than *Pteronotus* (11–18 *vs.* 27–39) and, of course, much shorter pulses than *C. parnellii*. Possibly the promptness of change in interpulse interval during the approach phase in *C. psilotis* is a direct result of the short range at which it detects fruit flies and the resultingly more clearly defined target.

The distance covered in the approach phase is similar in *C. psilotis* and *Pteronotus* since *C. psilotis* flies somewhat faster. A bat of such size may require this minimal distance in order to align itself properly to intercept a fruit fly. But in the terminal phase, the distance is markedly shorter in *C. psilotis* (90–160 mm. *vs.* 190–270 mm.). This may reflect more accurate identification of the insect's position by the end of the approach phase in the case of *C. psilotis* or may imply more information per pulse or may simply result from the greater flight speed or shorter range. That is, the difficult problem may be to line up on the fly during the approach phase. The task of the terminal phase may simply be to keep the fly's position identified while one covers the intervening distance. It is possible that the differences which we see in length of pursuit may simply reflect the relative adaptedness of *C. psilotis* to detecting, pursuing, and/or catching fruit flies.

In both *C. psilotis* and *Pteronotus*, pulse duration decreases sharply during the approach phase. In both, the decrease is close to linear *vs.* time, implying that the bat is measuring distance from the target. If pulse duration were adjusted so as to give essentially equal amounts of pulse-echo overlap, then distance would, in effect, be measured. We have no direct evidence so far concerning how well a bat can discriminate time intervals or lengths of overlap. See discussion above.

There has previously been very little direct evidence of proportional measurement of distance in bats. Search phase pulse durations are presumably set so as to give pulse-echo overlap at a desirable hunting range. Unfortunately, our analyses are limited by having studied only one kind and size of target in the same room. In *C. parnellii*, the pulse duration during the approach phase rises and then falls, but in doing so accomplishes the same result as that in the other two bats—constant pulse-echo overlap. Here, too, a measurement of distance is implied. And in the terminal phase, pulse duration falls linearly *vs.* time.

Apparently either fixed amounts of pulse-echo overlap are useful during the

approach phase or some quantity proportional to pulse-echo overlap is being held constant purposefully. The degree of overlap is comparable in *C. psilotis* and *Pteronotus* but is some 15 times longer in *C. parnellii*. This is a striking difference in such closely related bats but its significance eludes us.

During the approach phase, the longest interpulse intervals in all of these bats are about 40–50 msec., followed by or alternating commonly with intervals of about 25 msec. before shortening sharply to values of about 5–7 msec. at the beginning of the terminal phase. Such regularity suggests that these interpulse intervals represent the reaction times for decisions of decreasing complexity as well as the need for increasingly frequent information. These two features—more frequent information *vs.* more thorough digestion and judgment of the information may well be segregated during the pursuit. In a pursuit which in all consumes substantially less than a second, *Pteronotus* may emit over 40 pulses. A tempting suggestion would be that the bat, detecting an interesting echo for the first time, might turn on an ordered and predetermined sequence of pulses of varying parameters and run through such a sequence without having to make more than a few intermediate decisions. Examining the various pursuits, however, we find that they are similar but non-congruent in almost every respect. The different number of pulses (total and in each phase), the different pulse durations, repetition rates, and total pursuit durations all imply a large number of intermediate decisions. At least two decisions, the duration of a later pulse and of a later interpulse interval, seem necessarily to be made after at least each of the early approach pulses. Later, the frequent pairing of pulses in terms of duration and the final steadiness of the interpulse intervals in the terminal phase may indicate a reduction in the number of decisions being made per pulse. The number of intermediate decisions involved in arriving at the desirable pulse duration and interpulse interval cannot now be assessed. But, in any event, about 50 to 60 msec. seem to be available in the early approach phase, about 10 msec. in the late approach phase, and about 5 msec. in the terminal phase in *C. psilotis* and *Pteronotus*. The times are slightly different in *C. parnellii*. Information is rapidly accumulating on the times involved in acoustic pathways in the central nervous system of bats but does not seem ready to permit useful speculations on the length of the paths involved here (Grinnell, 1963a, 1963b).

Interpulse intervals are essentially the same during the terminal phase in both *C. psilotis* and *Pteronotus* and may well be at the limit of muscle and nerve physiology in these as well as in *C. parnellii* (2.5 msec.). A final repetition rate approaching or exceeding 200 pulses/sec., as in *C. psilotis* and *Pteronotus*, clearly implies rapid contraction and relaxation of sound-producing musculature (Novick and Griffin, 1961; Revel, 1962). Repetition rates of this order of magnitude seem to be the limit in bats (Griffin, 1958). In addition to the physiological limitations of the musculature and nerves involved, the limit may also be imposed to prevent overlap of echoes with subsequent pulses.

Henson's (1964) recent studies of cochlear microphonics and stapedius muscle activity in *Tadarida* (Molossidae), a free-tailed bat, have suggested additional possible interpretations of some aspects of repetition rate in insect pursuits. In this bat, the stapedius muscle may contract some 6 to 15 msec. before pulse emission, when the pulse repetition rate is 50/sec. or less. At higher repetition rates,

60 to 80/sec., stapedius muscle contractions occur 4 to 8 msec. before pulse emission. At even higher repetition rates, 100–140/sec., stapedius contraction is continual. Such contractions reduce cochlear microphonics to a degree that implies about 20 db attenuation of incoming sound. Stapedius relaxation appears to be initiated within 1–2 msec. and complete by 10 msec. after the beginning of pulse emission at low repetition rates. At the higher repetition rates, the stapedius may remain contracted for up to 40 msec. after the end of the pulse train.

At low repetition rates, stapedius relaxation occurs rapidly enough for echoes from nearby objects to evoke larger cochlear microphonic potentials than do the outgoing pulses (Henson, 1964). Now, during the search phase, when echoes would presumably be faint and would occur unpredictably, there might well be advantage to having full stapedius contraction during the bulk of the outgoing pulse, with considerable relaxation at the time of echo reception (for example, during the last millisecond in *C. psilotis*). This design feature would interact with pulse duration since the pulse would have to last long enough to allow some stapedius relaxation. During the approach phase, the intensity and timing of the echo can be anticipated to some degree but may well have to be assessed carefully and, of course, the echo will still be relatively faint since the fly is from 100 to 500 mm. away. Thus the repetition rate may be kept low to allow maximum contraction of the stapedius during pulse output and relaxation during echo input, yielding protection and relative amplification alternately. By the end of the approach phase, at least two general features will have changed. The echo will have been substantially identified—the target located—and the echo will be predictable in time. Such anticipation of echo timing can improve perception of the echo. In addition, the target will be close, less than 150 mm., so that the signal will be physically more intense. These advantages may well permit sacrifice of stapedius relaxation and substitution of high repetition rate. At such close range auxiliary factors reducing the apparent intensity of the outgoing sounds (acoustic isolation of the ear capsule, directional pinnae, etc.), central facilitation (Grinnell, 1963a, 1963b), and increasing echo intensity might all combine to give satisfactory signal:noise ratios. Note, too, that the intensity of pulses during the search and approach phases ought to be greater than during the terminal phase because of the greater range. There is little objective evidence of absolute intensities during these pursuits since the distance and orientation of the bat relative to the microphone have not been recorded. Bats which routinely must hunt at short target ranges, however (Nycteridae and others), use low intensity pulses (Novick, 1958) while bats which routinely hunt at long distances (*Rhinolophus* and *C. parnellii*) use high intensity (Novick and Vaisnys, 1964). High intensity output would also favor maximum stapedius contraction and relaxation during the search and approach phases while less contrast would be required during the terminal phase.

Lastly, one should consider whether the frequency pattern exemplified by *C. psilotis* reflects simply coordination of the cricothyroid muscle with the stapedius muscle. Novick and Griffin (1961) have shown that cricothyroid muscle action potentials can be recorded, from several genera of bats, which have timings relative to the emitted pulses very similar to those of *Tadarida* stapedius muscles (Henson, 1964). If these two systems are designed to work together, the rapid responses required may have led to development of reflex association of the muscles involved

so that the frequency pattern and/or the duration of the pulses during the various portions of the pursuits may be set by the needs of stapedius contraction and relaxation.

In summary, repetition rate during search and approach phases might be set to allow time for stapedius contraction and relaxation, in order to clarify echo perception. In the terminal phase, when echoes would be more intense, stapedius relaxation appears to be surrendered in favor of rapid repetition rate.

What determines the ultimate pulse duration in the terminal phase in these three species has not been clarified. In *C. psilotis* and *Pteronotus*, pulses of 1 msec. and shorter characterize this phase. Shorter pulses occur in insect pursuits in vespertilionids (Griffin, 1962; Webster, 1963) and in the general emissions of many other bats (Novick, 1958, 1963a), but the pulses seen here are, nevertheless, very short and may represent the best that the physical apparatus of these bats can deliver. On the other hand, in these three species, we have substantial circumstantial evidence that pulse-echo overlaps are essential to insect pursuit and that the useful amount of pulse-echo overlap in *C. psilotis* and *Pteronotus* is about 1 msec. If, indeed, they depend on such overlap, the limits on pulse duration are set. The vespertilionids apparently avoid overlap by using pulses as short as 0.3 msec. or less. All insectivorous bats, vespertilionids as well as chilonycterines, must be very close to an insect ultimately in order to capture it. We do not yet have sufficient information on the actual range between the ear and the mouth and the insect in any species of bat at the moment of capture though there are well documented examples of bats capturing insects in their wing membranes or inter-femoral membranes (Webster and Griffin, 1962). Such cases involved large insects and usually unnatural situations, however, and did not include our chilonycterines. But if a vespertilionid can avoid pulse-echo overlap up to the last moment by using pulses of 0.3 msec. and a chilonycterine uses pulses of about 1 msec., we may conclude, independently of other calculations, that in the last moments of a pursuit, *C. psilotis* and *Pteronotus* are still getting about 0.7 msec. of pulse-echo overlap.

Even though the terminal phase occupies only a very short time, during which the bats travel only a short distance compared with the distance covered in the approach phase, pulse duration must still decrease (and, indeed, it does) if pulse-echo overlap is to be held steady. At the very end of the terminal phase, pulse duration may flatten out or even fluctuate a bit. This may be evidence of the relatively great effect of the movement of the fly at close range and/or variation in the physical site of capture (wing, mouth, etc.). In *C. parnellii*, where there would seem to be greater leeway to shorten pulse duration without losing pulse-echo overlap or overtaxing the sound producing mechanism, the pulse duration seems to continue to decrease linearly (in pairs) throughout the terminal phase.

In all, these comparative data cast some light on the design of pulse duration, pulse repetition rate, pulse number, detection range and pursuit duration in these three species of bats during searching and during insect pursuits. We need more information on frequency pattern, intensity, flight speed, and the echolocation of targets of different sizes and velocities in order to reach more definitive conclusions. We would also benefit from more information about the natural prey and hunting habits of each of these bats.

SUMMARY

1. Elements of the acoustic orientation of *Chilonycteris philotis* during insect pursuits have been observed and analyzed. Such pursuits can be subdivided into search, approach, and terminal phases. The search phase is characterized by pulses of about 4 msec. duration repeated at a rate of about 18/sec. On detection of an insect, apparently by pulse-echo overlap (at a typical range of about 400–700 mm.), the approach phase begins, characterized by shortening (linear *vs.* time) pulse duration (to about 1.5 to 2.1 msec.) and shortening interpulse intervals. The approach phase (which lasts about 150–290 msec.; 5–9 pulses) ends in a transition to the terminal phase—a rapid sequence of short (1-msec.) pulses produced at a rate of about 170/sec. The terminal phase lasts about 50–94 msec. and includes 11–18 pulses. Constant pulse-echo overlap of about 1.2 msec. characterizes the approach phase, implying distance measurement and overlap utility. During the terminal phase, pulse-echo overlap appears to be set at about 0.8 msec. The pulses of *C. philotis* consist of a fundamental frequency, initially of about 21 kcps, accompanied by its second, third, and fourth harmonics. During the search phase, the initial and final 1.5 msec. of each pulse are of constant frequency but the central portion shows a frequency drop (for the fundamental about 4 kcps). During a pursuit, the constant frequency portions are shortened and then fused into the frequency modulated portion so that they are no longer recognizable beyond the early part of the terminal phase. Such a frequency pattern suggests possible mechanisms for recognizing and using pulse-echo overlaps.

2. The parallel parameters of *Pteronotus* and *Chilonycteris parnellii* pursuits, previously studied chilonycterine bats, are tabulated and compared with *C. philotis*.

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